NIDIFICATION AND REPRODUCTION OF *PHANAEUS* SPP. IN THREE TEXTURAL CLASSES OF SOIL (COLEOPTERA: SCARABAEIDAE)¹

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ABSTRACT

Nesting and reproduction of 3 species and 1 subspecies of *Phanaeus* were compared in 3 different textural classes of soil. *Phanaeus vindex* constructed brood balls in each of the soil classes but as the clay content of the soils increased, the number of brood balls constructed increased. The depth to the brood balls below the soil surface decreased as the content of clay in the soil increased. Survival of *P. vindex* to the third-stage larva was zero in the soil classed as sand, 50% in loamy sand and 95% in sandy clay loam. *Phanaeus torrens niger* constructed brood balls only in the sandy clay loam soil, whereas *P. igneus* and *P. igneus floridanus* failed to construct brood balls.

Introduction

Dung beetles of the genus *Phanaeus* in Georgia are important vectors of certain nematode parasites of swine (Porter, 1939; Stewart and Kent, 1963; Fincher, et al., 1969a). Three species and 3 subspecies of *Phanaeus* occur in Georgia. *Phanaeus vindex* MacLeay occurs throughout the state but is not as common in north Georgia as in middle and south Georgia. Only 2 specimens of *P. vindex cyanellus* Robinson have been captured, and these were from Tift County (Fincher, et al., 1969b). *Phanaeus torrens niger* D'Olsoufieff occurs in a small area located in the adjoining counties of Baker, Calhoun, and Dougherty (Fincher, et al., 1969b). *Phanaeus igneus* MacLeay is found throughout the lower half of the state below the Fall Line (roughly a line drawn through Columbus, Macon, and Augusta). *Phanaeus igneus nigrocyaneus* MacLeay has been seen only in a small sandy area of Tift County and on Blackbeard Island. *Phanaeus igneus floridanus* D'Olsoufieff is found in the southeastern counties of the state.

Members of the genus *Phanaeus* are the only dung beetles in the United States which form balls of feces underground and coat them with a thin layer of soil. The apparent protective nature of the outer hard shell suggests that soil type, distinguished primarily by texture, could be an important factor in the distribution of these beetles. Soil maps of Georgia indicate that *P. torrens niger*, *P. igneus nigrocyaneus* and *P. igneus floridanus* are limited in their distribution by soil type. Such is the case with the Jamaican species *Phanaeus carnifex* (Linnaeus), which is restricted to the red laterite or bauxitic soils of the island (Halffter and Matthews, 1966).

This report describes results of an experiment comparing nesting and reproduction behavior of 3 species and 1 subspecies of *Phanaeus* in 3 different

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textural classes of soil. The experiment was performed on a swine pasture of the Coastal Plain Experiment Station, Tifton, Georgia.

MATERIALS AND METHODS

Three $1.8 \times 1.8 \times 1.8$ m pits were excavated and each was filled with either sand, loamy sand, or sandy clay loam soil. These soils were classed according to their texture as determined by a particle-size analysis revealing the percentages of sand, silt, and clay. The sand was purchased from a local construction company and consisted of 91.0% sand, 0.6% silt, and 8.4% clay. The loamy sand was obtained from a local housing contractor and was composed of 72.0% sand, 13.6% silt, and 14.4% clay. The sandy clay loam was the subsoil of the other 2 pits and contained 62.0% sand, 11.6% silt and 26.4% clay. Each test plot was partitioned into quadrates by thin sheets of steel which were attached to wooden boards and driven approximately 75 cm into the soil. The sides of the pits were lined with galvanized metal which also extended 75 cm into the soil. The top of the metal was attached to a square wooden frame lying flush with the soil surface.

Fifty pairs of *P. vindex* were placed in a quadrate of each soil class as were 25 pairs of *P. igneus* (Fig. 1). Six pairs of *P. igneus floridanus* were used in a quadrate of each soil class. Eight male and 12 female *P. torrens niger* were placed in a sandy clay loam quadrate, 4 males and 8 females were put in a loamy sand quadrate and 7 males and 6 females were placed in a sand quadrate. Additional beetles of the latter 2 species were not available at the beginning of the experiment. A screen top (5.5 squares per cm) placed 20 cm above the soil surface over the quadrates prevented the beetles from escaping.

Fresh swine feces were always available to the beetles in each quadrate until burial activity ceased. The beetles were placed in the quadrates during the week of 14-20 September 1969, and the test plots were dug the following February to depths of 2 m. Most larvae in the brood balls recovered from the test plots were reared to adults in an environmental chamber.

RESULTS

Twenty-three brood balls were recovered from the sand quadrate containing *P. vindex*. Their location below the soil surface ranged from 50 to 75 cm, averaging 60 cm. No live larvae were found in any of these brood balls, and larval remnants indicated that death occurred early in development. No brood balls were found in the quadrates of sand containing other species.

The loamy sand quadrate containing *P. vindex* yielded 56 brood balls. The location of these brood balls ranged from 25 to 60 cm below the soil surface, averaging about 40 cm deep. About one-half of these brood balls contained live larvae. Larval remains in the other brood balls indicated that most had died during the 3rd larval stage. No brood balls were found in the quadrates of loamy sand soil containing other species.

One hundred and fifteen brood balls were found in the sandy clay loam quadrate containing *P. vindex*. The brood balls were located from 5 to 40 cm below the soil surface, averaging 25 cm. One hundred and eight of these brood balls contained viable larvae. The quadrate containing *P. igneus floridanus* revealed 21 brood balls, but overwintered adult *P. vindex* were also found. The galvanized metal and sheet metal were not properly joined between the 2 quadrates, permitting *P. vindex* to enter the quadrate containing *P. igneus*

floridanus. Adult *P. vindex* only were reared from the brood balls from this quadrate. The latter brood balls were found 15 to 35 cm below the surface.

The sandy clay loam quadrate containing *P. torrens niger* yielded 10 brood balls but only 4 contained live larvae and these were reared to adults in the laboratory. The *P. torrens niger* brood balls were constructed at about the same depth as those of *P. vindex*. No brood balls were found in the sandy clay loam quadrate containing *P. igneus*.

DISCUSSION

Of the 4 species, P. vindex was the only one able to construct brood balls in each of the 3 textural classes of soil. Such behavior parallels its wide distribution throughout the state in areas of widely differing soil types. Previous reports indicate that P. vindex brood balls occur at depths of 30 to 100 cm (Stewart and Davis, 1967) or in the first 10 to 15 cm of clay (subsoil) averaging 70 cm below the topsoil (Fincher, 1972). The present results however, showed that the average depth of the brood balls was less than 70 cm, even in the quadrate containing sand. Apparently the nearness of the subsoil to the surface was not the factor determining location of brood balls which would have been found at depths of at least 1.8 m in the sand and loamy sand plots of the present experiment. Therefore, P. vindex must rely on factors other than the depth to the subsoil below the soil surface for locating the brood chamber. Soil temperature and moisture content of the soil may be determining factors. However, crowding or other factors limiting the normal food finding and nidification behavior of the beetles in the present study must be considered in determining a "normal" depth for brood ball construction. The location of P. vindex brood balls in the same soil types under natural conditions may be quite different.

Dessication appears to be a major limiting factor in the reproduction of P. vindex. Twenty-three brood balls were constructed in the sand plot but no progeny survived. The brood balls were very dry and brittle when handled. Soils containing large amounts of sand are too permeable to retain large amounts of water. The moisture fluctuates greatly because large voids occur between adjacent soil particles. Dehydration during a drought period probably caused the death of the larvae in the brood balls coated with sand. Although P. vindex is found in sandy areas of the state such as the coastal counties, the population is not as great as that in inland counties with soils containing less sand. The high water table in the coastal counties provides moisture for the sandy soils throughout the year which may account for the survival of P. vindex in these areas.

The lack of nidification behavior of *P. igneus floridanus* in the quadrate containing sand is difficult to understand because they are found only in sandy areas of the state. This subspecies occurs in the Atlantic Coast Flatwoods which is in the southeastern portion of the state, roughly paralleling the coast and extending 80 to 140 km inland. The surface soils of this area range from sands to loams and that of the subsoils from sands to clays.

The results from quadrates of the remaining 2 soil textures indicate that the greater the content of silt and clay, the greater the chances of the larvae reaching the adult stage. The increase in clay content increased the water holding capacity of the soil and perhaps triggered *P. vindex* to construct more brood balls. One hundred thirty-six brood balls were constructed by *P. vindex* in the sandy clay loam quadrate which was more than double the number

constructed in the loamy sand quadrate. Also, 56 *P. vindex* brood balls were found in the loamy sand quadrate compared to 23 in the sand quadrate. The number of beetles were the same in each quadrate but the relative survival of adult beetles is unknown. Survival to the third-stage larva in the brood balls from the sandy clay loam plot was 95% compared to 50% in the loamy sand and

zero in the sand plot.

The sandy clay loam contained the greatest percentage of clay and instigated the greatest production of brood balls by $P.\ vindex$. Although $P.\ vindex$ constructed brood balls at an average of only 25 cm below the soil surface, 95% of them contained live larvae. Most Georgia soils have varying depths of topsoil containing less clay than the subsoil directly beneath. The depth of the topsoil, according to its physical characteristics, may determine the depth of brood ball construction.

The nidification behavior of *P. torrens niger* was as expected. Brood balls were constructed only in the quadrate containing the sandy clay loam because this species occurs in an area with little or no topsoil. The clay content of the scant topsoil ranges from 20 to 35% and that of the subsoil is above 37%.

Three environmental factors appear to be interrelated in influencing the production of brood balls and survival of larvae. Soil permeability decreases with an increase in clay content, fostering a decrease in moisture and temperature fluctuation. The soil usually dries from the surface downward. Normally, there is an increase in water content as the depth of the soil increases. The increase in water content increases soil density and the thermal capacity by volume. The thermal conductivity of wet sand and clay are similar; however, the range of thermal conductivity for dry sand is narrow when compared to that of dry clay which is relatively broad (Geiger, 1965). Furthermore, stabilization of soil temperature occurs with increased soil depth regardless of soil texture. Greater temperature fluctuations occur at ground level than at points a few centimeters below the soil surface. Geiger (1965) stated that temperature fluctuations on an undisturbed summer day in Leipzig, Germany, ranged from 14 to 40°C at the soil surface, but, at a depth of 35 cm, the temperature range was only 16 to 17°C. A much more elaborate experiment than the present one would be required to generate sufficient data to detect the role played by each of these factors and to estimate the effects of other factors.

50 Male	25 Male
50 Female	25 Female
P. vindex	P. igneus
6 Male	8 Male
6 Female	12 Female
P. igneus	P. torrens
floridanus	niger

50 Male	25 Male
50 Female	25 Female
P. vindex	P. igneus
6 Male	4 Male •
6 Female	8 Female
P. igneus	P. torrens
floridanus	niger

50 Male	25 Male
50 Female	25 Female
P. vindex	P. igneus
6 Male	7 Male
6 Female	6 Female
P. igneus	P. torrens
floridanus	niger

SANDY CLAY LOAM

LOAMY SAND

SAND

Fig. 1: Arrangement of the Test Plots (number and species of beetles indicated in each quadrate).

Conclusions

Soil type, distinguished primarily by texture, is an important factor governing the distribution of the dung-burying *Phanaeus*, although only 2 of the observed species formed brood balls. The brood balls of *P. igneus* and its subspecies were not observed, and it is assumed that conditions necessary for nidification behavior were not met. Behavioral differences between *P. vindex* and *P. igneus* have been previously noted (Stewart, 1967; Fincher, et al., 1971). The interspecific differences apparently are much more complex than can be assumed by external morphological similarities.

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BOOK NOTICE: Insects of the World, by Walter Linsenmaier. (Translated from the German by L. E. Chadwick) 1972. McGraw-Hill Book Co., 1221 Avenue of the Americas, New York, N. Y. 10020. 8½ × 11", 392p., thousands of illustrations: cloth \$25.00

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